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CONVERGENCE CAUSED CONFUSION: ON THE SYSTEMATICS OF THE FRESHWATER GASTROPOD *SULCOSPIRA PISUM* (BROT, 1868) (CERITHIOIDEA, PACHYCHILIDAE)

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ABSTRACT

We document a case of shell convergence in sympatric freshwater cerithioidean gastropods that has caused confusion in traditional classifications emphasizing shell features. Based on the comparative study of the operculum, radula, and embryonic shell obtained from dry remains of soft bodies, we present evidence that "*Melania*" *pisum* is not a thiarid species closely related to *Balanocochlis glans* (Busch, 1842), as has been supposed with respect to the very similar shells of both species. The species is transferred to the family Pachychilidae, because it shows various typical character states for the family. It is tentatively placed within the genus *Sulcospira*, which is endemic to Java. We assume that a similar shell shape has evolved in both species of not closely related gastropods through convergence, which once more reveals that purely shell-based classifications are particularly problematic.

Key words: Cerithioidea, Thiaridae, *Balanocochlis*, Java, molluscan shell, convergence.

INTRODUCTION

Molluscan shells have been particularly emphasized in classical systematic treatments. Indeed, shells bear many features that are convenient for taxonomic purposes, especially at the species level. An important aspect is that shell features are accessible also from dry material, which still represents the majority of museum holdings. In addition, dry shells often constitute taxonomically or historically important lots, such as types. Consequently, the importance of shell features for the recognition of taxa is also acknowledged in modern systematic works (e.g., Smith, 1981; Ridgway et al., 1998; Vermeij & Snyder, 2006), as well as in field guides. On the other hand, the shell is particularly prone to different kinds of environmental pressures (Vermeij & Covich, 1978; Reid, 1986, 1992; Warner, 1996; West & Cohen, 1996; Reed & Janzen, 1999), which may lead to the evolution of convergent traits, as shown even for relatively complex shell structures, such as the clausilial apparatus (Moorsel et al., 2000).

Since the late 20th century, shell shape convergence in gastropods has increasingly been highlighted as causing considerable confusion in taxonomic and systematic studies as demonstrated by, for example, Davis (1979) showing convergences among pomatiopsid, hydrobiid, littorinid, and cerithioidean gastropods, West & Cohen (1996) and Strong & Glaubrecht (2003) for thalassoid paludomids in Lake Tanganyika, and by Albrecht et al. (2004) for patelliform basommatophorans.

The problem inherent to the traditional approach of studying exclusively dry shells is that no other sources of information are used to evaluate the diagnostic value of shell features regarded as being taxonomically informative. Surprisingly, not a professional scientist, but rather the poet Edgar Allen Poe (1809–1849) was among the first (if not the first) to recognize that a reliable determination and classification of molluscs requires a combined analysis of the shell and soft body anatomy (Poe, 1839). In his scholarly textbook, he also distinguished – one of the first to do so – between the terms conchology (the study of shells) and malacology (the study of molluscs). Unfortunately, Poe's insights were ignored for more than a century before first Keen (1936) and later Gould (1995) took notice of it. The study of Davis (1979) may

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be taken as a prime example of modern malacology, which seeks to combine detailed quantitative and qualitative anatomy, multivariate analyses and shell morphology to untangle problems confounded in earlier works by convergences in hydrobioid snails.

Also, in the polymorphic freshwater cerithioidean gastropods formerly subsumed under the term "melanians", for a long time shell features were almost exclusively used for the classification of supraspecific taxa. For example, Brot (1874) stated that a siphonate aperture was typical for the genus *Acrostoma* Brot, 1870 (synonym of the pachychilid genus *Paracrostoma* Cossmann, 1900; see Köhler & Glaubrecht, 2002). Later, Solem (1966) and Brandt (1974) suggested that *Paracrostoma* can be distinguished from the closely related genus *Brotia* H. Adams, 1866, by its generally conical shell. However, recent revisions demonstrated that in Pachychilidae there is no correlation between shell shape and other morphological characters (Köhler & Glaubrecht, 2001, 2003, 2005, 2006, 2007). Molecular and morphological evidence showed that similar shell forms (i.e., conical ones) reflect similar ecological adaptations rather than close relationship (Glaubrecht & Köhler, 2004). By contrast, it was shown that pachychilid species formerly treated as conspecific based on the possession of a similar shell can be differentiated by means of other morphological characteristics (e.g., Köhler & Glaubrecht, 2006). For a striking example of the systematic confusion arising from a deviant appraisal of shell features compare the influential view of Rensch (1934), Benthem Jutting (1956), and Brandt (1974), who assumed that *Brotia costula* (Rafinesque, 1833) is a widely distributed and morphologically plastic species, versus the revised concept of Köhler & Glaubrecht (2006). The latter authors delineated *B. costula* in a much more restricted way and removed numerous taxa with similar shells from its synonymy. With respect to both geographical distribution and morphological plasticity, the revised taxonomy revealed that the ranges of *Brotia* species are generally much more restricted than formerly assumed.

In the present paper, we address the systematic affinities of an enigmatic species with a confusing taxonomic history. Described as *Melania pisum* Brot, 1868, from Java, it has attracted little attention mainly because of its sparse occurrence in museum collections worldwide. *Melania pisum* was originally considered as a member of *Acrostoma* Brot, 1868 (Brot, 1874) (= *Paracrostoma*), but ignored by most subsequent authors. In the few accounts availabe, *M. pisum* was generally treated as a member of the Thiaridae Troschel, 1857, and either retained as a valid species within the genus *Balanocochlis* Fischer, 1885 (Leschke, 1914; Benthem Jutting, 1956), or considered as being conspecific with *Balanocochlis glans* (Busch, 1842) because of the similar shell (Köhler & Glaubrecht, 2002). All previous systematic treatments were, however, based solely on shell features. Comparative data, including shell morphometry, radular and embryonic shell morphology, show that *M. pisum* is clearly distinct form *Balanocochlis glans*. Furthermore, we present evidence that this species is not a thiarid, as formerly assumed, but member of the Pachychilidae, a family not recognized by most previous authors. Hence, although conchologically very similar to each other, the thiarid *Balanocochlis glans* and the pachychilid *M. pisum* – which is tentatively placed within the genus *Sulcospira* – are not even closely related. We assume that a similar shell shape has evolved in both species convergently, which once more reveals that purely shell-based classifications are particularly problematic.

MATERIALS AND METHODS

The study is based on the examination of dry shell material, including type material, from the Museum of Natural History, London (BMNH), the Geowissenschaftliche Sammlung, Universität Bremen (GSUG), the Muséum d'Histoire Naturelle, Genève (MHNG), the Natural History Museum Naturalis, Leiden (RMNH), the Museum of Comparative Zoology, Cambridge, Mass. (MCZ), and the Museum für Naturkunde, Berlin (ZMB).

Dimensions of adult shells were measured with a calliper precise to 0.1 mm using standard parameters as detailed by, e.g., Köhler & Glaubrecht (2006). Shell dimensions (H – height, B – breadth, LA – length of aperture, WA – width of aperture, BW – height of body whorl, N – number of remaining whorls) were statistically analysed with the statistic software SPSS vs. 12.0. Remains of soft bodies found in dry shells were watered before opercula, radulae, and embryonic shells were removed and cleaned mechanically (opercula and embryonic shells) or by proteinase K digestion (radulae). Radulae and embryonic shells were mounted on specimens stubs using adhesive pads, coated with gold-palladium and examined using a Jeol FSM 6300 scanning electron microscope.

SYSTEMATIC DESCRIPTIONS

Pachychilidae Troschel, 1857

Sulcospira Troschel, 1858

Sulcospira pisum (Brot, 1868), new comb.

Melania pisum Brot, 1868: 54–55, pl. 2, fig. 5; Brot, 1870: 323.
Melania (Acrostoma) pisum – Brot, 1874: 18, pl. 1, fig. 7.
Melania (Balanocochlis) pisum – Leschke, 1914: 251.
Balanocochlis pisum – Benthem Jutting, 1956: 384–385.
Balanocochlis glans [partim] – Köhler & Glaubrecht, 2002: 124.

Type Material: Lectotype, herein designated, and paralectotype MHNG (ex coll. Brot, "Java"). Size of the lectotype [mm]: H = 14.2, B = 10.0, LA = 5.1, WA = 10.1, BW = 12.9, N = 2.5.

Other Material: Four dried shells MNHG (ex coll. Brot, "Java, leg. Schepman"); 40 dried shells RMNH 106883-4 ("Java, ex coll. Junghuhn, Reg.Nr. 2204, det. Van Benthem Jutting"); nine dried shells MCZ 346541 ("Java", leg. Schepman, ex coll. Junghuhn, ex RMNH).

Taxonomic Remarks: The species was first described by Brot (1868) from material collected by Petit (Brot, 1874: 18). The shell depicted here in Figure 1A is designated as the lectotype of *Melania pisum* Brot, 1868, in order to preserve stability of nomenclature according to the stipu-

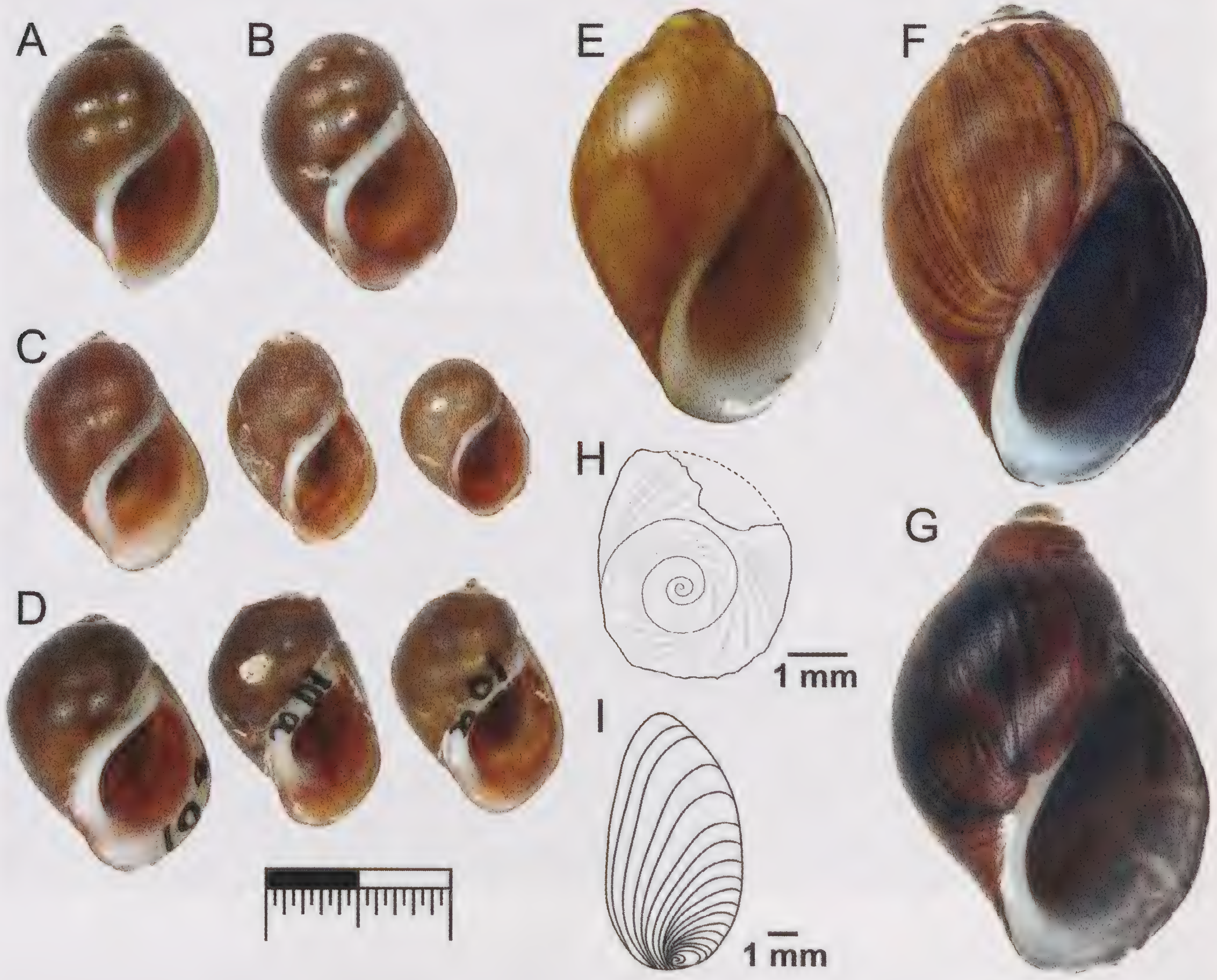

FIG. 1. Shells (2x natural size). A: Lectotype of *Melania pisum* MNHG, Brot collection (Java); B: Paralectotype MNHG, Brot collection (Java); C: Three shells MNHG, Brot collection (Java); D: Three shells RMNH 106884 (Java); E: Syntype of *Melania glans* Busch, 1842 GSUG 14583; F: *Balanocochlis glans* ZMB 46.049 (SW Java, Palabuan); G: *Balanocochlis glans* ZMB 102.695 (New Ireland); H: Operculum of *S. pisum* RMNH 106884; I: Operculum of *B. glans* ZMB 46.049 (Java). Scale bar for shells = 10 mm.

lations of § 74.7 of the *Code of Zoological Nomenclature* (ICZN 1999). The paralectotype is depicted in Fig. 1B. There is a second lot in the Brot collection (MNHG) comprising four shells collected by Schepman as is evident from the label on the cardboard onto which the shells were mounted. Being of a deviant provenance, these shells are not considered as types. Later, Brot (1874) affiliated *M. pisum* with the genus *Acrostoma* Brot, 1870, and stated that a siphonate aperture is characteristic for this group. Because the name *Acrostoma* was preoccupied, the valid name of the genus is *Paracrostoma* Cossmann, 1900 (Köhler & Glaubrecht, 2002). Based on close conchological similarity with *Balanocochlis glans*, *M. pisum* was also considered a thiarid. Leschke (1914) and Benthem Jutting (1956) retained *pisum* as a valid species within *Balanocochlis* (to be distinguished from *B. glans* and *B. glandiformis* by a more globular shape of the body whorl and generally smaller size), whereas Köhler & Glaubrecht (2002) suggested that it may be a junior synonym of *B. glans*.

Shell Morphology (Fig. 1A–D): Comparatively small, with a globular shape. Spire always truncated with usually less than three remaining whorls. Body whorl large compared to rest of shell, accounting for around 90% of entire shell height, inflated, and convexly rounded in diameter. Scupture smooth except for growth lines. Colour chestnut brown, sometimes with darker vertical flames or lines. Aperture with thick col-

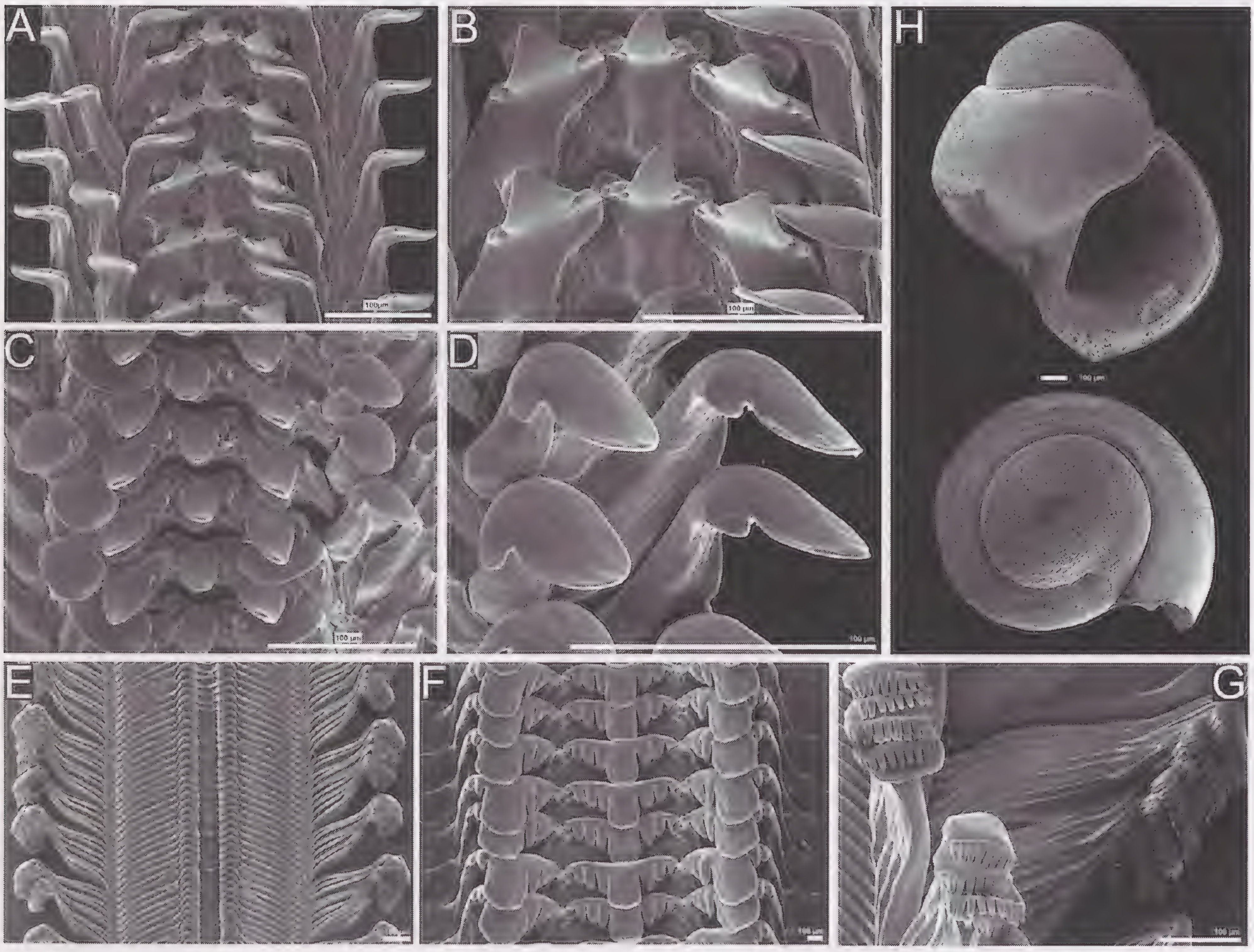

FIG. 2. Radular and embryonic shell morphology. A–D: SEM images of a radular fragment of *S. pisum* extracted from dry shell material (RMNH 106884). A: View from above; B: Detail showing central and lateral teeth; C: Anterior viewed obliquely at 45° from above showing the shape of radular denticles; D: Detail showing marginal teeth; E–G: SEM images of a radular fragment of *B. glans* extracted from dry shell material (BMNH 2128; Solomon Ils., Guadalcanal). E: View from above; F: Detail showing central and lateral teeth; G: Detail showing lateral teeth; H: SEM images of embryonic shell of *S. pisum* (RMNH 106884), front view (above) and apical view (below). Scale bars = 100 µm.

umellar margin, wide, laterally and terminally rounded, pointed above; lower margin being conspicuously protracted. Average size (n = 52, median and standard deviation in parentheses): H = 11.24 (1.57) mm, B = 8.32 (1.06) mm, LA = 4.36 (0.66) mm, WA = 7.77 (0.96) mm, BW = 10.46 (1.54) mm, N = 1.5 (0.61).

Operculum: Ovate with almost a central nucleus, comprising four to five whorls (RMNH 106883-4, various opercula of corresponding shape).

Embryonic Shell Morphology (Fig. 2E): Brot (1874) found embryonic shells in one of the types comprising two whorls and exhibiting spiral colour bands. The whereabouts of these shells are unclear. We found three embryonic shells in the remains of one dried body (RMNH 106884) with a height of about 1.2 mm comprising 1.5 whorls. Sculpture is smooth, with faint growth lines. Apical whorl is inflated and dome-like.

Radula (Fig. 2A–D): Two radula fragments isolated from dry remains of soft bodies (RMNH 106884) showed exactly the same morphology. The radula is taenioglossate, typically pachychilid. Seen from above, central teeth are squarish; their cutting edge consists of a pronounced main cusp flanked by three accessory cusps that taper in size. Their upper rim is convex, their lower rim is concave by the extending glabella. Marginal margins of the glabella are only slightly concave. Lateral teeth possess a triangular-shaped main cusp with two to three outer and one inner accessory cusp, their outer lateral margin supports a lateral flange, ventral surface with conspicuous glabella. Inner and outer marginals are hooked, each possesses a large, well rounded main denticle and a much smaller inner cusp. Outer marginals have a lateral flange at their exterior side.

Soft Body Anatomy: Unknown for the lack of preserved material. The presence of embryonic shells shows that *S. pisum* is a brooder.

Distribution: All known material originates from Java; more precise locality information is not available from the historical museum material. Recent efforts by the authors and their collaborators to find the species in the field were not successful thus far.

DISCUSSION

Freshwater Cerithioidean Gastropods – Sketching the Systematic Framework

Tropical cerithioidean freshwater gastropods, currently known to represent several distinct freshwater radiations, were originally held to represent one large monophyletic group. This group was initially called the melanians (or Melaniidae), but later renamed Thiaridae because the generic name *Thiara* Röding, 1798, has priority over *Melania* Lamarck, 1799 (reviewed in Glaubrecht, 1996, 1999, 2006). Later recognized as polyphyletic, this group was progressively split into various distinct families, each of it characterized by typical radular, operculum, and soft body characteristics. These lineages are also recognized in molecular phylogenetic studies (Glaubrecht, 1996, 1999, 2006; Lydeard et al., 2002; Köhler et al., 2004). This led to a more restricted definition of the true Thiaridae and the delimitation of further freshwater lineages, such as the Pachychilidae, which were previously not widely accepted (reviewed in Köhler & Glaubrecht, 2002). These changing systematic concepts and the inconsistent use of taxonomic names have caused considerable confusion. Today we know that the true Thiaridae and the Pachychilidae are only distantly related to each other, representing lineages that colonized freshwater independently (Lydeard et al., 2002; Köhler et al., 2004). Their members are most easily recognized by means of their divergent – but within each family conserved – radula and operculum morphology (e.g., Köhler & Glaubrecht, 2001). Thiaridae generally possess a paucispiral operculum (Fig. 1I), whereas Pachychilidae always have a multispiral operculum (Fig. 1H). In addition, the radula shows a variety of marked differences, such as varying shapes and relative sizes of teeth (compare e.g. Fig. 2A–D with 2E, F).

Diagnostic Value of Shell Features in Freshwater Gastropods

Contrary to Poe's (1839) credo, in traditional classifications shell features were often exclusively used for the delineation of gastropod taxa. This holds true also for most freshwater cerithioideans, such as the species relevant in the context of the present study (*B. glans*, *S. pisum*). Their traditional placement within the Thiaridae merely reflects the unawareness of former workers that, in addition to the Thiaridae, there are further freshwater cerithioidean lineages while the affiliation of *M. pisum* with *Balanocochlis* by Leschke (1914) and Benthem Jutting (1956) solely rests on the postulate that a similar shell indicates close relationship (Fig. 1 compares these taxa). In fact, the shells of both species are similar in regard to their shape, colour, sculpture, and form of aperture. In illustrations of shells, Van Benthem Jutting (1956) showed the body whorl of *pisum* as being of a more globular shape compared to *B. glans*. However, the examination of a large series of shells revealed that *B. glans* is quite variable and that globular shells also occur in this species (Brinkmann & Glaubrecht, unpubl. data). More reliable than with respect to overall shell shape, both taxa can be discriminated by means of shell size parameters. One-way ANOVA revealed that shells of *S. pisum* differ from those of *B. glans* in regard to various morphometric parameters (H, B, LA, WA, BW, N, H/B, H/LA, H/BW) with statistical significance at the 0.1% level ($p < 0.000$). Re-classification of shells by discriminant analysis (one discriminant function, Wilk's lamda = 0.213, $p < 0.000$) resulted in 100% correct reassignment of *S. pisum* shells ($n = 52$) and 99.4% correct reassignment of *B. glans* shells ($n = 349$), thus strongly corroborating the results of the ANOVA (diagrammatically represented in Fig. 3). Thus, contrary to the assumption of Köhler & Glaubrecht (2002), our findings support the retention of *S. pisum* as a species distinct from *B. glans*, as suggested by Leschke (1914) and Benthem Jutting (1956). However, while the analyses of shell parameters demonstrate that close similarity does not imply identity in this case – the similar shells say nothing about the phylogenetic relationships of the species involved. Instead, we found that both species display marked morphological differences in the radula and operculum, which imply placement of each in distinct families (Thiaridae and Pachychilidae, respectively). Because the globular, almost limpet-like shape of shells is unusual in both families of freshwater cerithioideans, we assume that it has evolved in parallel – possibly due to adaptation to similar habitat conditions and lifestyles. Similar cases of homoplastic shell shapes have been reported from other Asian pachychilid species (Köhler & Glaubrecht, 2005, 2006), as well as further groups of freshwater gastropods (Davis, 1979; West & Cohen, 1996; Strong & Glaubrecht, 2003; Albrecht et al., 2004). Hence, whether shell features can be con-sidered as being of diagnostic value with respect to the systematic treatment of a given taxon has to be tested in the context of more comprehensive analytical work.

Systematic Implications

As stated above, the former systematic placement of *M. pisum* in the Thiaridae merely reflects the traditional treatment of freshwater cerithioideans (e.g. Thiele, 1928, 1929–1935; Leschke, 1914; Benthem Jutting, 1956). As judged from the presence of typical characteristics of the operculum and radula, however, only *B. glans* is a genuine member of this family (paucispiral operculum with basal nucleus; radula with comparatively small central teeth, lateral teeth with a large lateral flange, and marginal teeth with numerous cusps; Figs. 1, 2; see also Rensch, 1934; Benthem Jutting, 1956; Starmühlner, 1976; Glaubrecht & Brinkmann, unpubl. data). By contrast, *S. pisum* exhibits characteristics typical only for Pachychilidae. These include possession of a multispiral operculum with a central nucleus and a radula with pronounced central teeth, lateral teeth with a short lateral flange, marginal teeth with only two cusps. Also its embryonic shell closely resembles that of other Southeast Asian pachychilids (Köhler & Glaubrecht, 2001, 2005, 2007). Since *pisum* is evidently a pachychilid, it cannot be a member of the thiarid genus *Balanocochlis*. To deduce its correct generic placement within the Pachychilidae, however, is difficult. A molecular phylogenetic analysis of the Asian Pachychilidae showed that the morphological characteristics found to be typical for the entire family (radula, operculum) are widely conserved among its representatives and therefore not suitable to infer the generic placement of the present species (Köhler & Glaubrecht, 2001, 2002; Köhler et al., 2004). Instead, it was demonstrated that the genera of SE Asian Pachychilidae (*Adamietta*, *Brotia*, *Jagora*, *Paracrostoma*, *Sulcospira*, *Tylomelania*) essentially differ with respect to their reproductive anatomy (gonads, gonoducts, brooding structures) and, to a lesser degree in the embryonic shell morphology (Köhler & Glaubrecht, 2001, 2003, 2005, 2006, 2007; Rintelen & Glaubrecht, 2005).

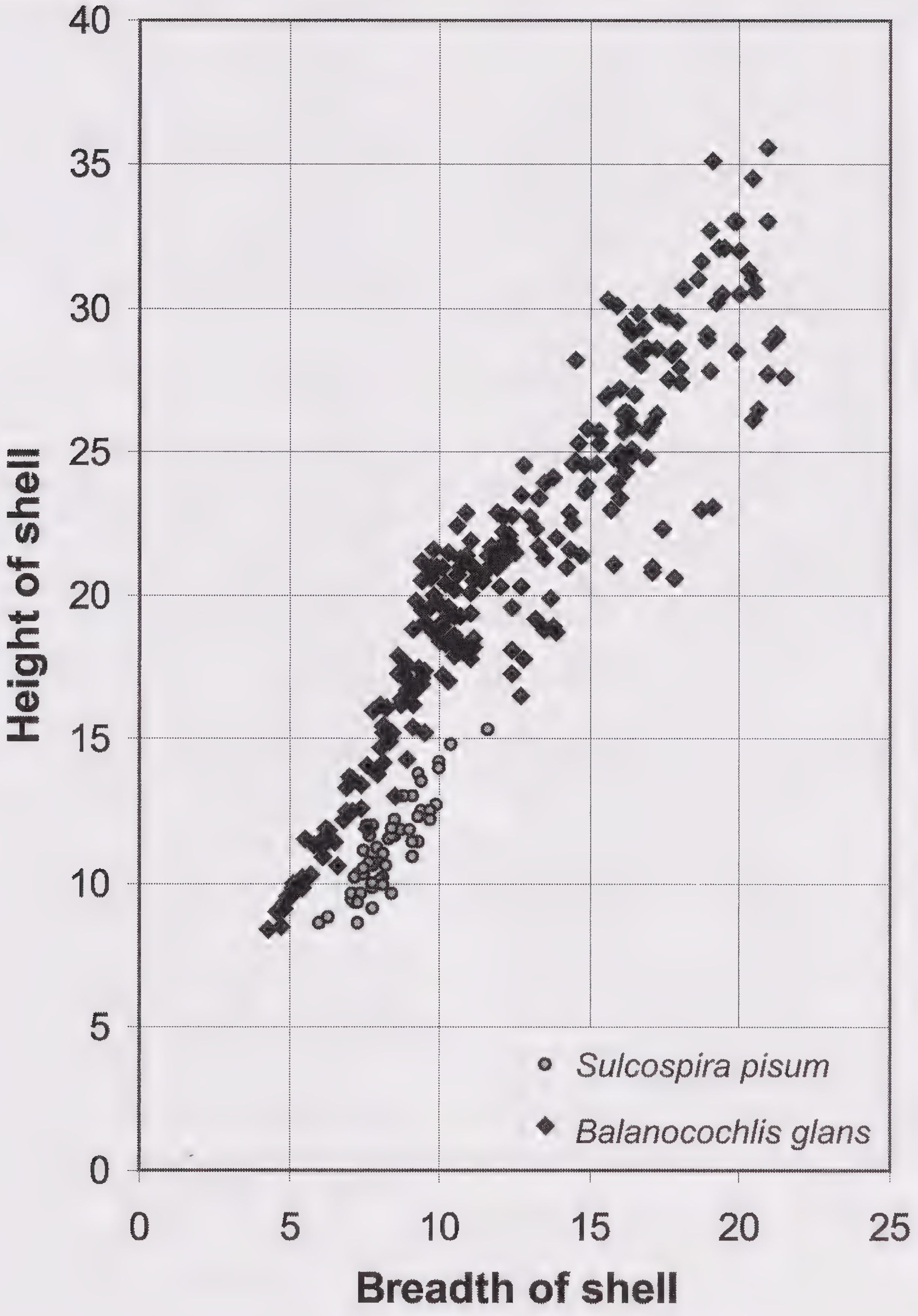

FIG. 3. Comparison of shells by means of the parameters height and breadth of the thiarid *Balanocochlis glans* (n = 154) and the pachychilid *Sulcospira pisum* (n = 52).

Because the reproductive anatomy of *pisum* remains unknown due to the absence of preserved material, it is not possible to reconstruct its generic affinities without ambiguity. A dome-like inflated embryonic shell with a smooth sculpture, as shown here for *pisum*, is known from a total of three pachychilid genera or groups: The so-called "*Brotia testudinaria*-group" (Köhler & Glaubrecht, 2001), the genus *Sulcospira* endemic to Java (see Köhler & Glaubrecht, 2005), and *Paracrostoma* endemic to India (Köhler & Glaubrecht, 2007). Because the "*Brotia testudinaria*-group" represents an informal grouping only, which awaits critical revision, and *Paracrostoma* is restricted to southern India, *Sulcospira* is currently rendered the only available generic name. Therefore, the pachychilid species *pisum* is here tentatively placed within this genus until a more detailed revision of all Javanan Pachychilidae becomes available.

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